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Forest stocks control long-term climatic mortality risks in Scots pine dry-edge forests

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Abstract. Forest research has addressed the importance of an improved understanding of drought–stocks interactions in the dry edge of tree species range. Nonetheless, more efforts are still critically needed to link up the multiple ways by which climatic stressors can trigger tree mortality, including population-level determinants and management. Here, we analyze the interactive effects of North Atlantic Oscillation (NAO), a surrogate of climatic variability in southwestern Europe, and forest stocks on tree mortality in dry-edge populations of the most widespread Eurasian tree species, *Pinus sylvestris* L., in the forest of Valsaín (central Spain). Specifically, we use tree mortality data gathered since 1941 in six multiannual periods. Results suggest that the main mortality risks in these forests can occur either in positive or negative NAO phases, but that their relative impacts are critically mediated by forest structure. In NAO^+ periods, commonly associated with warm–dry conditions in the Iberian Peninsula, a peak of mortality was found in closed forest sections, whereas the second peak, found in open forest sections, was related to NAO^- periods, correlated with temperate-rainy weather conditions. This finding reinforces the key role of management—through its control on forest structure—as a driver of forest vulnerability to climate. Accounting for the multiple ways in which stocks modulate tree responses to different risks emerges as a critical element when it comes to the design of efficient adaptation measures in managed dry-edge forests.

Key words: adaptation; climate change; dry-edge forests; *Pinus sylvestris*; Valsaín forests.

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Introduction

Forest structure and its associated functions and services may experience dramatic changes due to drought-induced tree mortality in water-limited environments (Allen et al. 2010). Interestingly, a number of empirical accounts have described tree mortality as a complex phenomenon that often results from synergies between a number of potential predisposing factors, such as tree crowding and/or insect outbreaks, together with climate (Franklin et al. 1987, Dale et al. 2001). In space, interactions between population-level determinants (such as

tree competition in dense stands) and climatic anomalies have revealed critical to define tree mortality patterns properly (Ruiz-Benito et al. 2013). In time, the interplay between different climatic stressors and tree stocks has nonetheless received less attention, mostly due to the difficulties to obtain suitable information on past population-level determinants and the scarcity of long-term mortality records in forests.

Drought is one of the most important plant stressors at the dry edge of tree species ranges worldwide (Allen et al. 2010). An intense drought can cause sudden tree die-off by inducing hydraulic failures and the collapse of vascular tissues (Anderegg et al. 2016). In isohydric species (i.e., in species having strong stomata regulation in response to water shortage), tree death during prolonged dry spells may also be attributed to carbon starvation (McDowell et al. 2011, Sevanto et al. 2014). Alternatively, intense/prolonged drought can trigger cascading processes that can lead to forest dieback eventually (Bigler et al. 2007, Hereş et al. 2012, Camarero et al. 2015). For instance, drought has been reported critical in triggering subsequent insect outbreaks as well as diseases and other pests (Wermelinger et al. 2008, Breshears et al. 2009). A number of tree-ring studies have evidenced this pattern after specific extreme drought pulses in temperate latitudes (e.g., Dobbertin and Rigling 2006). Yet, these studies usually did not account for neighborhood competition. In general, the upscaling of individual tree performance (in terms of radial growth responses) to infer tree mortality stand dynamics remains a challenge. It is therefore critical to analyze alternative information such as historical management archives to unveil how climate–forest stock interactions drive stand dynamics in dry-edge forests (Canadell and Raupach 2008).

At low latitudes, temperate and boreal species tend to inhabit mountain environments where abiotic determinants other than drought may play a role in tree mortality (Kajimoto et al. 2004, Barbeito et al. 2012). For instance, overexposure of individual trees to physical damage associated with snowfall, ice glaze, winds, and floods can raise mortality, particularly in dense stands where shadier conditions impose higher height:-diameter ratios (Won and O'Hara 2001). In these forests, windstorms pose a major threat and silviculture is oriented toward providing wind stable edges to felling areas (Mason 2002). Alternatively, at the dry edge, drought is considered a main threat (Herrero et al. 2013) and management here aims at controlling stand density to minimize competition during drought periods (Young et al. 2017). These two paradigms, however, may be in conflict when applied to Mediterranean mountains where populations of Eurasian species persist at the dry edge of their distribution and where both storms and droughts may play a critical role.

Here, we study the role of forest stocks (i.e., wood volume per hectare) in driving natural tree mortality of Scots pine (*Pinus sylvestris* L.) at its dry edge on the central Iberian Peninsula. We assess the interactive effects between forest stocks and climate over the past 70 yr in the forest of Valsaín (Spain), where Scots pine is the dominant tree species. We hypothesize that forest stocks correlate with increasing natural tree mortality by aggravating the deleterious effects of aridity during dry–warm periods (Ruiz-Benito et al. 2013, Young et al. 2017). Likewise, we hypothesize that this effect may be reversed during wet–cold periods due to the protection of tree crowding against winter storms, strong winds, and snow. To this end, we use the North Atlantic Oscillation (NAO) index as a climatic mode linked to atmospheric sea surface level pressures that relates to windstorms as well as patterns of temperature and precipitation variability at annual to decadal timescales (Trigo et al. 2004, López-Moreno et al. 2011, Madrigal-González et al. 2017, 2018).

Materials and Methods

Study area

The Valsaín pinewood (*Pinar de Valsaín*) lies on the northwestern slopes of the Guadarrama Mountains (*Sierra de Guadarrama*), in the central sector of the Iberian Central Range. Since 2013, this forest is part of the Peripheral Protected Area of the Sierra de Guadarrama National Park. The Valsaín pinewood covers a surface of 7448 ha spanning a rather steep elevation gradient from ~1200 to 1900 m asl (Fig. 1).

The climate is Mediterranean although summer aridity is progressively attenuated with increasing altitude due to lower temperatures and higher precipitation. At 1200 m asl, mean

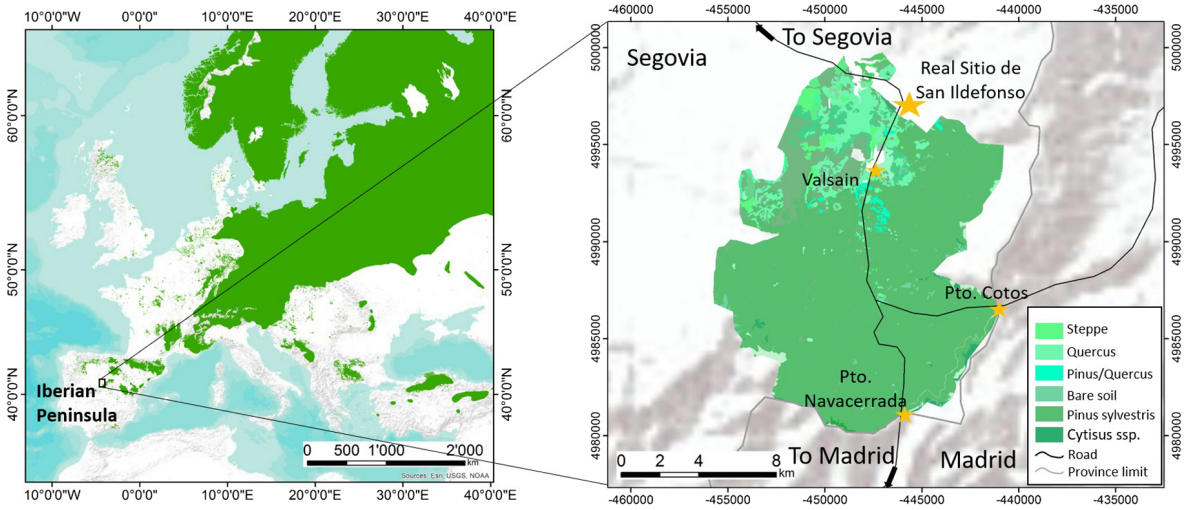

Fig. 1. Location of the study area on the Central Iberian Peninsula. The Valsaín forest is located on the northern slope of the Guadarrama Mountains (Spain).

annual temperature, T_{January}, T_{July}, and mean annual precipitation are 10°, 3°, 19°C, and 700 mm, respectively, whereas at 1900 m asl, values are 6°, −1°, 16°C, and 1300 mm, respectively. The typical Mediterranean summer drought is not particularly severe in this mountainous area of central Spain, lasting two months at low elevations and only one month in the summit areas. Vegetation mostly consists of dense natural stands of *P. sylvestris* L., with *Quercus pyrenaica* Willd, *Sorbus aucuparia* L., *Prunus avium* L., and *Ilex aquifolium* L. as the main accompanying tree species. Toward the low elevation limit of the forest, *Q. pyrenaica* becomes more abundant, particularly in the understory, whereas at the upper forest limit (tree line ecotone), the pinewood gets more open and mountain shrubs, such as *Juniperus communis* L. subsp. *alpina*, *Cytisus oromediterraneus* Rivas Mart., *Adenocarpus hispanicus* Lam (DC), and *Vaccinium myrtillus* L., are abundant in the understory. The main human activities in the Valsaín forest comprise extensive cattle ranching, pine logging, and recreational activities.

Forest management: shelterwoods in the Mediterranean

The Valsaín pinewood has been managed since 1889, that is, for more than a century. The main goal of forest management has traditionally been the production of high-quality timber of *P. sylvestris*, while, at the same time, guaranteeing protection against erosion/flooding, avoiding the occurrence of insect and pest outbreaks, and allowing cattle and horse ranching. Nature protection, landscape preservation, and recreational uses have substantially gained importance over the last decades. For management purposes, the forest is divided into three blocks (*secciones*) and eleven logging units (*cuarteles*), managed according to the floating block method. Nine of these units are mostly devoted to timber production, whereas the two remaining units are dedicated to recreational activities and protection against natural hazards (such as flooding, erosion, landslides, and debris flows). The production units are managed according to the shelterwood group selection silvicultural system, whereas the single tree selection system is applied to the protection and recreation units. Scots pine is a light demanding, shade intolerant species in most of its range, but in Mediterranean forests, regeneration can be low in exposed sites due to high summer seedling mortality. The shelterwood group selection silvicultural system approach guarantees proper regeneration, as seedlings benefit from partial shade during the dry summer, especially on south facing slopes. The approach is hence preferred over clear cutting for both ecological and social reasons. The rotation period is 120 yr for *P. sylvestris* in the Valsaín pinewood

for the logging units, with intermediate thinning to improve wood quality and to reduce competition in young stands. Finally, certain volumes of standing and lying deadwood are left at the site to promote biodiversity.

Forest and climate data

We used the historical shelterwood cutting data from the *Valsaín pinewood* recorded in each of the management plans carried out in 1941 (1941–1947), 1948 (1948–1957), 1958 (1958–1964), 1965 (1965–1988), 1989 (1989–1998), and 1999 (1999–2010). This dataset includes detailed information related to tree harvesting and the reasons of forestry interventions, with the latter being separated into ordinary causes (i.e., wood exploitation), drought, regeneration improvement, forest clearing, or extraordinary damage (Cabrera and Donés, 2010). These records therefore also include information on mortality and allow disentangling management-induced from natural mortality patterns. In the present work, we use the number of dead trees (natural causes only) registered between consecutive forest inventories and divided their number by the number of years of the time period under consideration. The information contained in the management plans covers all the extension of the Valsaín pinewood and is spatially aggregated at the logging unit level. This dataset, along with detailed management unit cartography, also provides a unique chronosequence to study the effects of forest structure on different ecological processes, including mortality. Based on this information, relative tree mortality was defined as the number of trees that died from natural causes (percentage, relative to the total number of trees at the beginning of a given period) per hectare and year (no.·ha^{-1}·yr^{-1}) at each logging unit. At the logging units, we obtained wood volume (m^3/ha) and used it as a surrogate of tree stocks derived from the management plans. Average elevation (masl) in each logging unit was derived from the existing Lidar Digital Elevation Model (DEM) data provided by the Valsaín pinewood authorities. Climate data were retrieved from different sources: Wind direction and intensity were obtained from the Navacerrada rain gauge station (40°47′ N, 4°00′ W, 1894 m asl) since 1946. In addition, we used the North Atlantic Oscillation (NAO) index as the major climate mode controlling weather conditions on the Iberian Peninsula (López-Moreno et al. 2011). The index is defined as the standardized difference of atmospheric pressure between Iceland and Gibraltar. In a situation where strengthened sea-level pressure favors the formation of a strong Azores High, westerly winds laden with moisture will be re-directed to central and northern Europe where they cause rainy–cold conditions. This same pattern will favor continental weather with dry–warm conditions and high temperatures in southern Europe (Trigo et al. 2002). In the situation where the sea-level pressure gradient between the Azores and Iceland weakens, the southern will experience rainy and comparably cold conditions. Ample evidence exists for an influence of the NAO on tree growth and forest productivity in southern Europe (Roig et al. 2009, Camarero 2011, Madrigal-González et al. 2017, 2018). In this study, we use NAO index data that were retrieved from the website of the Climate Research Unit at East Anglia (https://crudata.uea.ac.uk/cru/data/nao/nao.dat; Appendix S1: Fig. S1).

To quantify drought effects on tree mortality, we employed the standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) retrieved from https://spei.csic.es/map/maps.htmlmonths=1#month=2#year=2020. In addition, we analyzed correlations between the NAO index and winter precipitation data (accumulated precipitation from December to March, both months included) available from three meteorological stations located nearby the Valsain study area (i.e., Puerto de Navacerrada, Segovia [Zamarramala], and Rascafría). These data were retrieved at annual time resolution to demonstrate that the NAO indeed influences local climate significantly—as stipulated in literature.

Data analyses

We modeled tree mortality as a linear function of interactive effects between climatic variability (NAO) and tree stocks (wood volume at the logging unit level, hereafter WV, and tree density at the logging unit level, hereafter TD) using linear mixed models (LMM). We also included elevation in the LMM as a potential predictor of tree mortality (Van Gunst et al. 2016). Tree mortality data were log-transformed to meet normality

and homogeneity of variance. We considered the logging units in the management forest plans as a random term since all the measurements were periodically reported in the historical management updates at this spatial scale. Model selection was conducted using the Akaike information criterion corrected for small sample size (AIC_c, Hurvich and Tsai, 1989). Specifically, we started with a full model including WV, TD and elevation and the interaction between NAO and WV. In a first round, we removed TD, elevation, and the interaction NAO × WV one at a time and compared the resulting models with the full model using AIC_c. We discarded parameters when their elimination resulted in models with AIC_c no larger than four units compared with the full model AIC_c.

Variance inflation due to potential collinearities among the predictor variables was checked using the variance inflation factor. Error distribution was explored using graphical analysis (i.e., q-q plots and residuals vs. predicted values plots).

Finally, we analyzed relationships between the NAO and climatic elements of tree mortality such as precipitation and wind regime using Pearson's correlation test.

Results

Forest data from 1941 to 2010 show moderate mortality overall throughout the logging units, ranging from 0% to 7% trees·ha^{-1}·yr^{-1}. Tree mortality is, however, variable in space and time according to climatic variability and tree stock dynamics. The highest mortality rates are, on average, observed in the period 1948–1958 (3.5% trees·ha^{-1}·yr^{-1}), whereas the lowest values are found between 1941 and 1948 (1% trees·ha^{-1}·yr^{-1}; Fig. 2).

Interestingly, neither TD ($\Delta AIC_{c\ TD} = -6.4$) nor elevation ($\Delta AIC_{c\ elevation} = -5.6$) were supported as predictors of tree mortality in the Valsaín pinewood. In turn, the LMM supports the occurrence of interactive effects between the NAO and WV on tree mortality ($\Delta AIC_c = 9.3$; see parameter estimates in Table 1). This interaction indeed points to two major peaks of mortality (i.e., >5% trees·ha^{-1}·yr^{-1}), (1) one related to positive NAO phases in logging units with high tree stocks and (2) one related to negative NAO phases in logging units with low tree stocks (Fig. 3). The lowest tree mortality rates (i.e., <1 tree·ha^{-1}·yr^{-1}) occurred during positive NAO phases in open logging units.

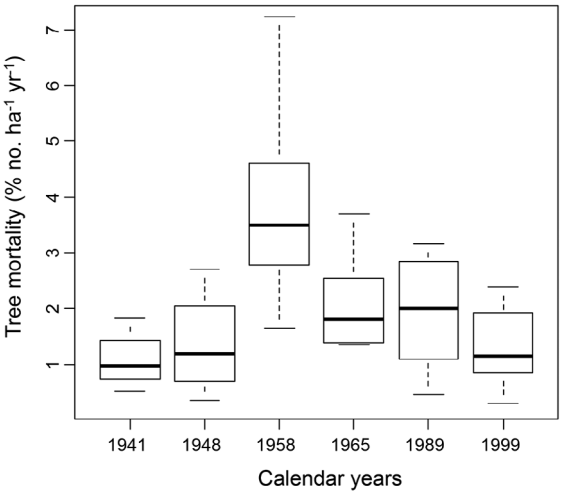

Fig. 2. Descriptors for tree mortality at logging unit level per multiyear period. The calendar years represent the initial year of the multiyear period with available data.

The Shapiro-Wilk normality test supported a normal distribution of residuals in the final model ($W = 0.978$, $P = 0.522$) and the graphical evaluation of residuals evidenced a lack of bias in the distribution of residuals along the predicted values (Appendix S1: Fig. S2). In parallel, correlation analyses strongly support the predominance of windy and humid weather conditions during predominantly negative NAO phases, and, on the contrary, calm and dry weather conditions when NAO phases are positive ($R = 0.92$, $P < 0.01$ for NAO wind; $R = -0.71$, $P < 0.01$ for NAO drought; see Fig. 4). Correlation analyses at annual time

Table 1. Parameter estimates for the supported mixed-effects model.

Fixed effects	Value	SE	df	*t*	*P*	vif
(Intercept)	0.945	0.083	37	11.451	0.0000	
NAO	−0.184	0.051	37	−3.593	0.0009	1.167
WV	0.082	0.055	37	1.502	0.1415	1.075
NAO × WV	0.337	0.078	37	4.325	0.0001	1.119

Note: NAO, North Atlantic Oscillation; WV, logging units wood volume; vif, variance inflation factor.

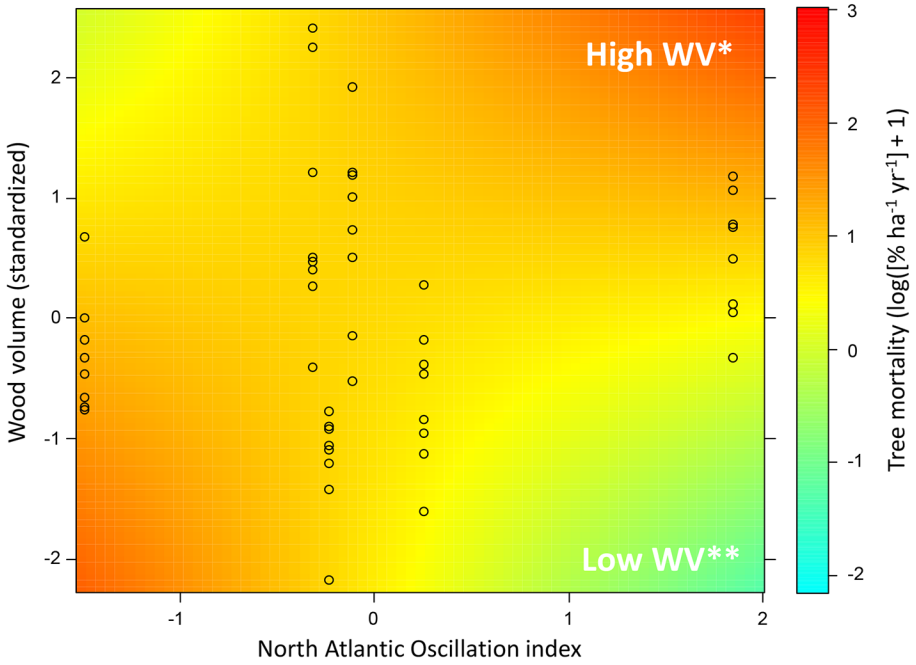

Fig. 3. Colored regression plot for tree mortality as a function of the North Atlantic Oscillation and discretized tree stocks (wood volume, WV m^3/ha) into high and low categories (above and below the median, respectively).

resolution from three meteorological stations nearby the Valsaín study site corroborate these results (see Appendix S1: Fig. S3).

Discussion

Results support a prominent role of climate–stock interaction in driving tree mortality in this mountain pinewood. Specifically, while the relationship between the NAO index and tree mortality is positive in logging units with high WV, the relationship turns negative when WV is low. By contrast, neither the effects of elevation nor TD affect tree mortality. Recent findings in a Mediterranean forest in North America reported that altitude drives tree mortality, with peaks of mortality in dense stands at low elevations where lower precipitation would lead to more intense competition for water and solar radiation (Van Gust et al. 2016). The lack of influence of elevation in our study might be attributed to the large size of the logging units (hundreds of hectares), which introduces relevant intra-logging unit variation in elevation that may blur up the mortality patterns associated with differences in elevation among logging units. A previous study on tree mortality on the Iberian Peninsula suggested that altitudinal mortality patterns (increased mortality with increasing altitude) could be explained by the low tolerance of Mediterranean tree species to cold temperatures and frost damage (Ruiz-Benito et al. 2013). Interestingly, *P. sylvestris* is an Eurosiberian tree species that reaches its southernmost limit in these Iberian forests. It is therefore not surprising that mortality rates do not increase significantly in a tree species that is so well-adapted to cold conditions when moving upwards within the study site. More so, resistance to cold temperatures in *P. sylvestris* has been observed even in early ontogenetic stages of development in northern latitudes (Rikala and Repo 1987).

One of the two peaks of tree mortality observed in the Valsaín pinewood occurs during the positive NAO phase associated with increased aridity due to blocking of North Atlantic storm tracks from reaching the Iberian Peninsula by the Azores high-pressure system (Trigo et al. 2002). This finding reinforces the role of drought as one of the main abiotic drivers of forest dynamics in temperate latitudes (Bigler et al. 2006). Accordingly, minimum tree growth and

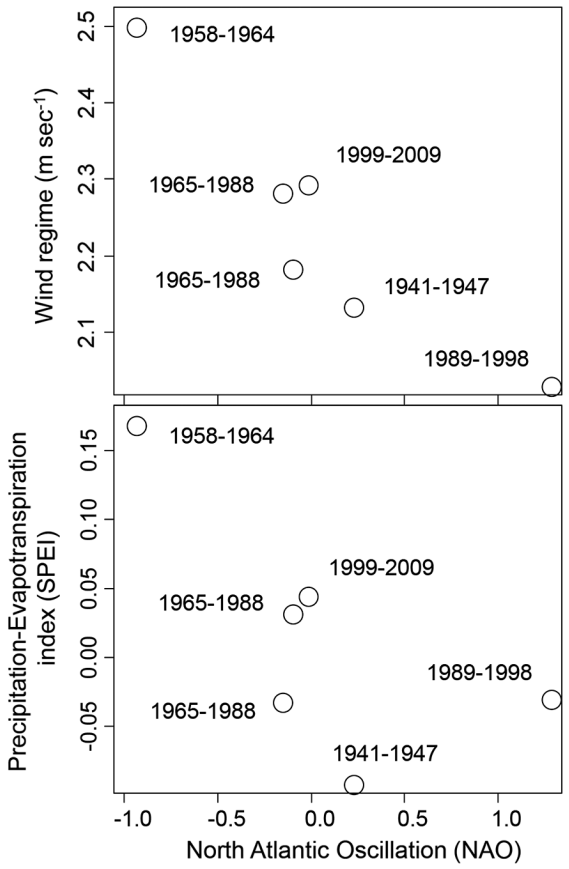

Fig. 4. Scatterplots for the relationships between the North Atlantic Oscillation (NAO) and wind regime (m/s) and standardized precipitation evapotranspiration index (SPEI).

forest productivity in Iberian pine forests occur during positive NAO phases throughout the 20th century (Madrigal González et al. 2017, 2018). On the Iberian Peninsula, a number of correlational studies have highlighted the important role of climate change-related droughts in triggering forest dieback in the past (Carnicer et al. 2011, Sánchez-Salguero et al. 2012, Hereş et al. 2014, Gea-Izquierdo et al. 2014). Further, on the one hand, some studies proved that the linkages between drought and latter tree defoliation are a complex phenomenon partly mediated by growing incidence of defoliating insects under rising temperatures and aridity (Carnicer et al. 2011). On the other hand, some studies showed that tree crowding can aggravate the negative impacts of drought by exacerbating water demand related to enhanced competition (Vilà-Cabrera et al. 2011).

Results show quite clearly that increased standing biomass correlates to higher tree mortality during drier periods, thus supporting the aggravating role of crowding in drought-induced mortality. Forest densification has been proposed as one of the most important predisposing factors to mortality in water-limited environments for *P. sylvestris* (Vilà-Cabrera et al. 2011, 2013, Ruiz-Benito et al. 2013) and other species with similar ecological requirements such as *Abies pinsapo* (Linares et al. 2009). For this reason, moderate thinning has been proposed as an appropriate management strategy to reduce tree mortality through alleviating water stress locally (Vilà-Cabrera et al. 2011, but see Camarero et al. 2011). At the same time, results also support a peak in tree mortality during predominantly negative NAO phases. In Mediterranean-type climates, precipitation is more abundant during autumn and winters with prevailing negative NAO phases, in turn related to an increased frequency and intensity of winter storms. At the study site, this is indeed evidenced by the strong negative relationship between wind speed and the NAO ($R = -0.92$). Classical works suggest that wind is a major ecological factor affecting tree fitness and survival in mountain areas (Ennos 1997), where it can indeed interact with forest stocks in a similar way than snow or ice glaze, thereby promoting tree mortality. This means that trees with too high height:diameter ratios will be more vulnerable to strong winds due to trunk instability, and mortality rates should therefore be higher in crowded forest stands (Wonn and O'Hara 2001). Additionally, previous research in the study area supports a significant increase of flash flooding events causing notable tree mortality associated with sudden snow melting and heavy rain during negative NAO phases (Ballesteros-Cánovas et al. 2015). Surprisingly, our results point to opposite trends, with tree mortality rising during negative NAO in open forest sections. Classical models suggest that in dense stands, tree stability of average trees tends to decrease as the height:diameter ratio increases, which is usually a major consequence of stem over-elongation due to shady conditions imposed by canopy trees (see, e.g., Vospernik et al. 2010). This implies that in denser

stands, less stable trees—usually average and suppressed trees—are more prone to fail under strong winds, snowfall, and ice glaze (Won and O'Hara 2001). Nonetheless, our results may still be reconciled with classical forest ecological knowledge considering a potential trade-off associated with shelterwood thinning practices in Mediterranean forests. On the one hand, sequential thinning over a period of 30–50 yr promotes tree regeneration and provides protection to seedlings against summer drought via shading. On the other hand, shading induces high height:diameter ratios in juvenile pine trees. As thinning progressively reduces the density of old trees, saplings with high height:diameter ratios become more and more exposed to winter meteorological events and wind. Alternatively, one might consider that less crowded forest sections of the Valsaín pinewood cover bare rocky soils on steep slopes at high elevation where trees are more exposed to wind, snow, and ice glaze than forest sections on gentler slopes with more developed soils where tree density is much higher. Nonetheless, trees in naturally open forests tend to invest more into radial than longitudinal growth, with a typical stocky architecture that is often a good adaptation to overexposure to wind and snow (Poorter et al. 2003, Lines et al. 2012).

Our findings provide relevant clues for the application of traditional shelterwood thinning (i.e., adaptation measures) in this and other *P. sylvestris* dry-edge populations under ongoing climate change. Indeed, the multi-faceted climate–stock interactions driving tree mortality represent a major challenge for the coming decades. On the one hand, increased aridity will impose further restrictions to growth and extended rotation periods will probably be needed to ensure recruitment survival and growth under the canopy of mature trees (Linder 2000). On the other hand, the observed trade-off will simultaneously expose the less crowded sections to increased risk of mortality as a likely consequence of too high height:diameter ratios in saplings due to their development in shaded environments for longer time periods. Climate change adaptations may imply changes in the thinning calendar, for example, through an advancement of secondary preparatory thinning to avoid plastic adjustments under shade conditions. These procedures are more related to timber quality and maybe adequate for specific productive forests but should be revisited when elevated risks can jeopardize the benefits. A thorough review of the optimum tree densities along the management calendar is thus needed to minimize tree mortality due to winter events while maintaining acceptable survival rates during prolonged/intense dry spells. Our results are also relevant for proper design and parameterization of dynamic global vegetation models (e.g., Medvigy and Moorcrof 2012), particularly in the rear edge, suggesting interactions between episodic climatic induced mortality and tree density.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3201/full